THE EFFECT OF CONSTANT CONDITIONS OF LIGHT AND DARKNESS ON THE DIURNAL RHYTHM OF THE DISTAL RETINAL PIGMENT OF THE CRAYFISH *FAXONELLA CLYPEATA*

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One adaptation of crayfish to environmental conditions is the migration of the distal retinal pigment in the compound eyes from a distal position to a proximal one or vice versa. In the eye of an animal adapted to darkness, this pigment is in a distal position or dark-adapted condition. In the eye of an animal adapted to light, the distal retinal pigment moves proximally, away from the cones and is known as the light-adapted state. Exner (1891) believed that the pigment migration was a mechanism for regulating the amount of light entering the eye during the day and night, thus producing optimum vision under either condition.

Parker (1897) used a technique to observe the position of the distal retinal pigment in which the shrimp, *Palaemonetes vulgaris*, was fixed in hot water, the heads removed, and eyes sectioned. Welsh (1930) was the first investigator to develop a technique for measurement of the rate of distal retinal pigment migration in living specimens. He found that in the shrimp, *Palaemonetes vulgaris*, the distal retinal pigment migrated from a dark-adapted to a light-adapted condition in 40 to 50 min and from the light-adapted condition to the dark-adapted state in 80 to 90 min. Parker (1932) concluded from available evidence that retinal pigmentary changes had little adaptive significance except for responding to the general changes in illumination that occurred in the environmental day-night cycle.

Kiesel (1894) was the first to observe a daily rhythm of retinal pigment migration in an arthropod. He found the glow from the eyes of moths kept in darkness was greater by night than by day. The first report of a 24-hr rhythm of retinal pigment migration in a crustacean was published by Welsh (1930). He found a 24-hr rhythm of retinal pigment migration in *Macrobrachium olfersi*, and *M. acanthurus*, fresh water shrimps of Cuba. Bennitt (1932) reported a daily variation in the position of the proximal pigment of the eye of the crayfish, *Orconectes virilis*, when kept in constant darkness. Welsh (1941) illustrated the 24-hr cycle in retinal pigment migration with diagrams of the eye of the crayfish, *Cambarus bartoni*, showing the size of the pseudopupil.

The study described below was undertaken to determine (1) if the crayfish, *Faxonella clypeata*, has a diurnal rhythm of distal retinal pigment migration under constant conditions of light and darkness, (2) the effect of exposing the diurnal rhythm of the distal retinal pigment to different time periods of light and darkness, and (3) the effect of reversed illumination on the diurnal rhythm of the distal retinal pigment.

MATERIALS AND METHODS

The experimental animals were the crayfish, *Faxonella clypeata*, (Hay), collected at Pearl River, Louisiana. The crayfish, collected at frequent intervals to minimize the effect of maintenance in the laboratory upon the retinal pigment, were kept in aquaria containing aerated tap water. Specimens for each experiment were taken from the stock supply without regard to sex or size. Experimental crayfish were not fed.

Techniques used by most investigators were time consuming and, therefore, not favorable for the collection of data from large numbers of animals. The

method devised by Sandeen and Brown (1952), however, obviated this difficulty and was used to determine quantitatively the state of the distal retinal pigment. A crayfish was immersed dorsal side up in a dish of tap water on the stage of a stereoscopic dissecting microscope equipped with an ocular micrometer. The crayfish were viewed by transmitted light at a magnification of 60×. Each unit of the ocular micrometer at this magnification was equivalent to 25.3 μ. Under these conditions (fig. 1) a distal clear area was visible in the eye of light-adapted animals because of the proximal migration of the distal retinal pigment. The proximal edge of the clear area marks the outer limit of the distal retinal pigment. With the aid of the ocular micrometer the width of the clear area (A) and the distance from the surface of the eye to the apex of the notch at the proximal end

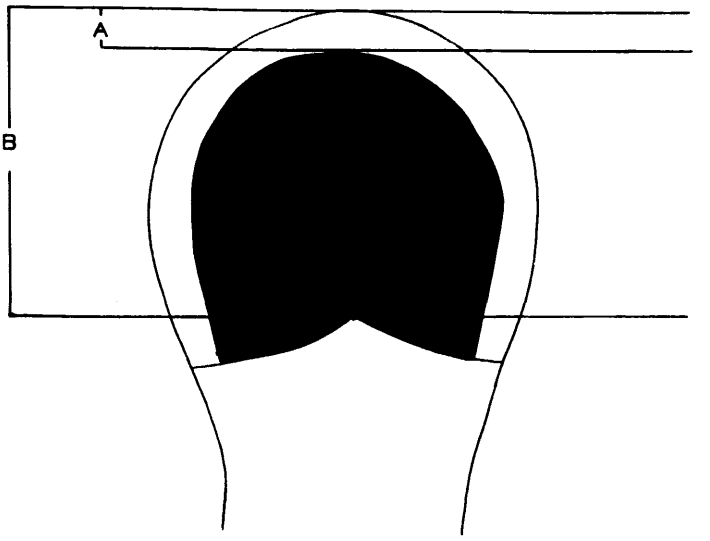

FIGURE 1. Diagram of the dorsal surface of an eyestalk of *Faxonella* to illustrate the method of determining the distal retinal pigment index.

of the eye on the dorsal surface of the eyestalk (B) were measured. The ratio A/B was than calculated and is referred to as the distal pigment index (D.P.I.). The value of the first measurement (A) decreases as the distal retinal pigment of the animals becomes dark-adapted while the second (B) remains constant for any one animal. Use of this ratio minimized variation in the results due to size differences of the individual crayfish because the value of both measurements varies with the size of the animal but the ratio of A to B varies principally with the degree of light adaptation.

A typical figure for the fully light-adapted state obtained in this manner would be 3/38 or a D.P.I. of 0.08. This technique of direct measurements was so simple that the condition of the distal retinal pigment of 10 crayfish was regularly determined in 3 to 5 min.

White enameled pans used for the experimental crayfish had a bottom diameter of 14.5 cm and contained aerated tap water approximately one inch deep. Experiments designed to determine the changes that occur during a period of time after subjecting the crayfish to an experimental condition were performed by exposing every pan to the same conditions. When darkness was desired a photographic

darkroom was utilized and the stock aquaria or pans used in the experiments were covered by black cloth at all times. The cloth was folded in such a manner that it was light-tight and one crayfish could be removed without illuminating the remaining crayfish.

The laboratory used for the experiments was air-conditioned and thus temperature was held relatively constant. Welsh (1941) observed daily changes in the pseudopupil of crayfish maintained at 21 to 23 C for four months and at 6.8 C for five months before the daily changes became difficult to distinguish. Brown and Webb (1948) showed that the frequency of the rhythm of melanophore pigment migration in the fiddler crab, *Uca*, was not altered but the amplitude was by temperatures between 6 and 26 C. At temperatures below 6 C the rhythm was inhibited.

EXPERIMENTS AND RESULTS

Diurnal Rhythm of Migration of the Distal Retinal Pigment of Faxonella

A preliminary experiment had shown that the distal retinal pigment had a diurnal rhythm of migration under normal day-night illumination. The following observations were made to determine if the distal retinal pigment would still exhibit a diurnal rhythm under constant conditions of light and darkness. Specimens of *Faxonella clypeata* were freshly collected for these observations. In the evening of the day of collection, 15 crayfish were placed into each of 12 pans, six pans were then placed under an illumination of 11 ft-c; the remaining ones were placed in the darkroom. At 9 AM the next morning the distal pigment indices of 10 crayfish in a pan from the darkroom and one from the 11 ft-c illumination were determined. The average D.P.I. of 10 crayfish, one pan in darkness and one under constant illumination, was determined again at 11 AM and at two hour

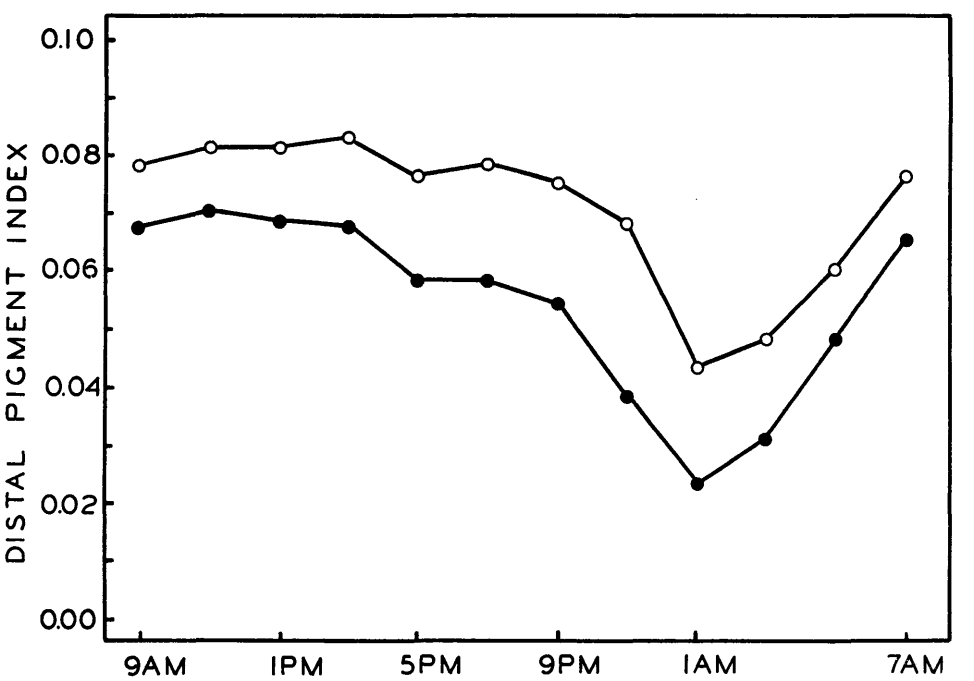

FIGURE 2. The diurnal rhythm of the distal retinal pigment of *Faxonella* under constant illumination, 11 ft-c (circles), and in darkness (dots).

intervals thereafter for 20 hr. The six pans were used in sequence, thereby the same crayfish would be used only once every 12 hr. An effect of the microscope light used in determining the distal retinal pigment index was thereby minimized. In the preliminary experiments in which the crayfish were discarded after each reading, the shape of the curves were identical to the one in which the crayfish were used only once every 12 hr.

TABLE 1

Results of experiments to demonstrate a diurnal rhythm of movement of the distal retinal pigment under different conditions of illumination.[1]

Experiments[2]		N	Range	Mean	S.D.
1. Light	1 PM	20	0.06–0.11	0.081	0.016
	1 AM	20	0.00–0.09	0.430	0.026
Darkness	1 PM	20	0.05–0.10	0.068	0.014
	1 AM	20	0.00–0.08	0.024	0.028
2. April 22					
Light	11 AM	15	0.07–0.10	0.086	0.012
	11 PM	15	0.00–0.07	0.023	0.021
Darkness	11 AM	15	0.07–0.12	0.079	0.017
	11 PM	15	0.00–0.07	0.013	0.020
April 25					
Light	11 AM	10	0.06–0.09	0.083	0.010
	11 PM	10	0.03–0.07	0.054	0.016
Darkness	11 AM	10	0.04–0.10	0.073	0.021
	11 PM	10	0.00–0.08	0.045	0.028
April 26					
Light	11 AM	10	0.07–0.10	0.083	0.013
	11 PM	10	0.03–0.07	0.055	0.015
Darkness	11 AM	10	0.06–0.08	0.070	0.007
	11 PM	15	0.03–0.05	0.036	0.015
3. Aug. 7–Sept. 4					
	8:30 AM	120	0.03–0.09	0.065	0.010
	1:30 PM	120	0.05–0.10	0.074	0.013
	4:30 PM	120	0.05–0.10	0.070	0.010
Sept. 5–Sept. 9					
	8:30 AM	30	0.06–0.10	0.075	0.009
	1:30 PM	30	0.06–0.09	0.071	0.008
	4:30 PM	30	0.06–0.10	0.075	0.010
4. Oct. 4	9 AM	10	0.05–0.07	0.058	0.013
	1 PM	10	0.06–0.08	0.068	0.008
	5 PM	10	0.04–0.07	0.054	0.008
Oct. 18	8 AM	10	0.06–0.09	0.077	0.010
	10 AM	10	0.04–0.06	0.050	0.007
	5 PM	10	0.05–0.07	0.058	0.008
Oct. 21	9 AM	10	0.06–0.09	0.072	0.009
	Noon	10	0.03–0.07	0.054	0.014
	5 PM	10	0.05–0.08	0.068	0.013
Oct. 25	8 AM	10	0.05–0.07	0.064	0.008
	11 AM	10	0.04–0.06	0.052	0.008
	5 PM	10	0.05–0.09	0.070	0.010
Nov. 1	8 AM	10	0.04–0.07	0.058	0.012
	11 AM	10	0.06–0.08	0.066	0.008
	5 PM	10	0.03–0.07	0.054	0.014
Nov. 8	8 AM	10	0.05–0.07	0.056	0.008
	1 PM	10	0.06–0.08	0.070	0.006
	5 PM	10	0.05–0.07	0.064	0.008

[1]N, number of pigment indices used in the calculations and S.D., the standard deviation.

[2]1. Diurnal rhythm in conditions of light and darkness.
2. Effect of time on diurnal rhythm.
3. Constant illumination for 34 days.
4. Effect of reversed illumination.

The experiment was repeated once. The data are presented in figure 2 where each point represents the average D.P.I. of 20 crayfish. The standard deviations in table 1, were based on the 1 PM and 1 AM readings. Specimens of *Faxonella* demonstrated a daily diurnal cycle of movement of the distal retinal pigment under constant illumination and constant darkness. The shape of the curve was the same in light and darkness but the animals in darkness had a lower degree of light adaptation throughout the diurnal cycle.

Effect of Time on the Diurnal Rhythm of the Distal Retinal Pigment

Since the whole curve is moved downward for the animals in constant darkness, the following experiment was conducted to determine the effect of seven days of constant illumination and darkness on the diurnal rhythm.

Three pans each containing 15 specimens of *Faxonella* from the stock aquaria

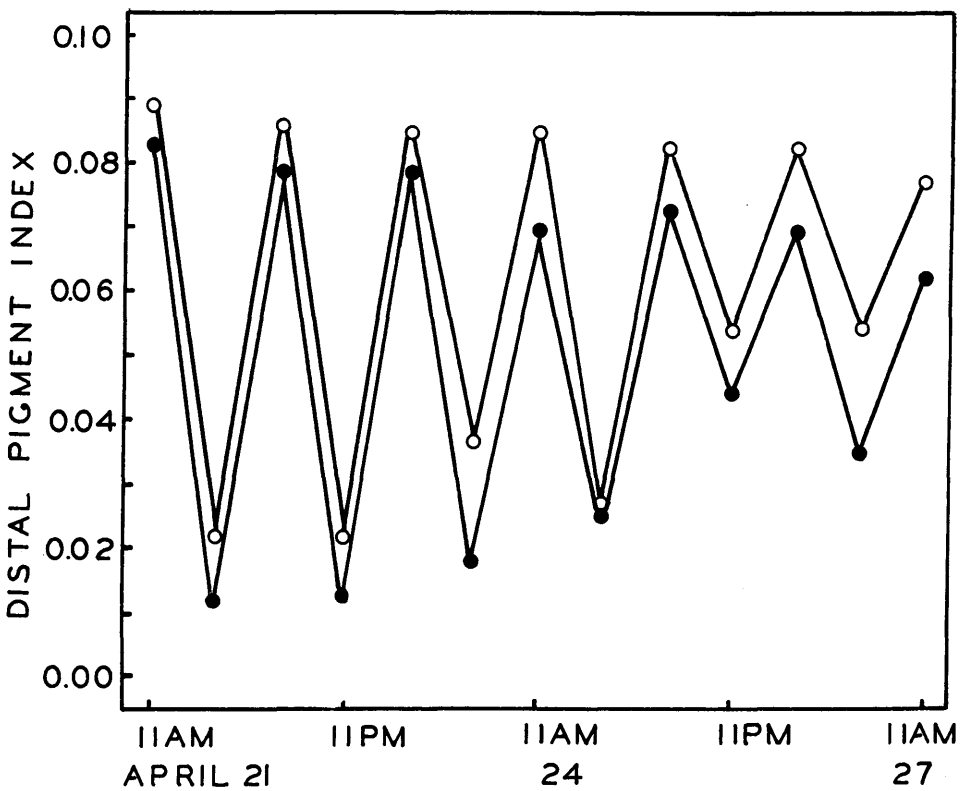

FIGURE 3. The diurnal rhythm of the distal retinal pigment of *Faxonella* under constant illumination of 11 ft-c (circles) and in darkness (dots).

were placed under artificial illumination of 11 ft-c and three pans with a like number of crayfish were placed in darkness. The average D.P.I. of 10 crayfish from the pans in the light and in the dark were determined at 11 AM and 11 PM each day from April 21 to April 27. The pans in darkness were used in sequence so that no pan was used at 11 AM and 11 PM of the same day.

The results of this experiment are presented in figure 3 where each point represents the average D.P.I. of 10 crayfish. The calculations in table 1 were based on the readings made for April 22, 25, and 26. The distal retinal pigment of cray-

fish under constant illumination continued to be maximally light adapted at 11 AM but the distal retinal pigment progressively became more light adapted at night. The distal retinal pigment of crayfish kept in darkness tended toward an intermediate state of light adaptation at all hours of the 24-hr day. Seven days of illumination caused the distal retinal pigment to progress toward a constant light-adapted state but seven days of darkness caused the distal retinal pigment to progress toward an intermediate state of light adaptation.

To ascertain what effect constant illumination would have on the frequency of the distal retinal pigment diurnal rhythm, 15 animals were placed into a pan under artificial illumination of 11 ft-c for 34 days. During this period the average D.P.I. of five crayfish was determined at 8:30 AM, 1:30 PM, and 4:30 PM an average of three days a week.

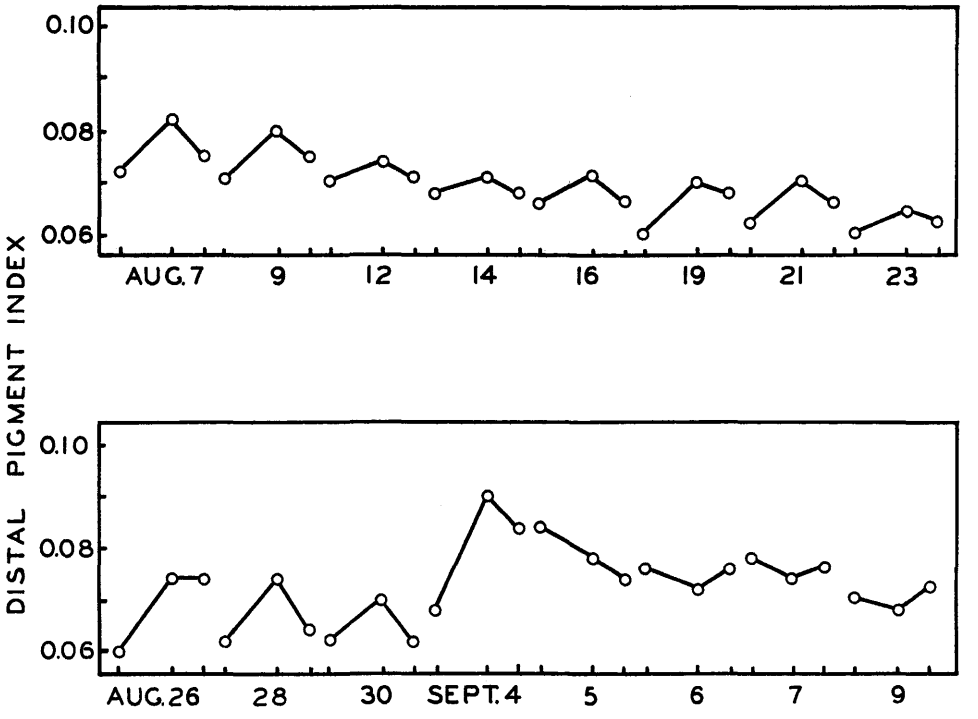

FIGURE 4. The distal pigment indices of *Faxonella* subjected to constant illumination of 11 ft-c. The average distal pigment index was determined at 8:30 AM, 1:30 PM, and 4:30 PM.

In figure 4 are depicted the results of this series of observations. The calculations in table 1 were based on the readings from August 7 to September 4, which were similar in nature and from September 5 to 9, which indicated a change in the diurnal rhythm. The value of the maximal D.P.I. of these crayfish exposed to constant illumination decreased with time. The diurnal rhythm persisted for 30 days. On the 30th day (Sept. 5th) the rhythm became abnormal, the 1:30 PM determination that normally was maximal was minimal. This condition was observed for the remaining four days of observation. The variation in the D.P.I. was so slight that inhibition of the rhythm by the light was suspected. This result was to be expected since the D.P.I. of crayfish exposed to seven days of illumination tended toward a light-adapted state (fig. 3). R. Smith (1948) ob-

served that the 24-hr retinal pigment rhythm in the crabs *Hemigrapsus oregonensis*, *H. nudus*, and *Pachygrapsus crassipes* was inhibited under constant illumination, the pigment remained in a continuously light-adapted state.

Effect of Reversed Illumination on the Diurnal Rhythm of the Distal Retinal Pigment

The experiment described above indicated that the diurnal rhythm was effected by illumination. The following series of experiments was undertaken to determine if the diurnal rhythm could be reversed by illuminating the crayfish at night, but not by day and if so could the rhythm be reverted to the original condition. Freshly collected animals were (1) subjected to reversed illumination for 17 days, (2) then kept in darkness for 10 days, and (3) finally placed in a normal day-night condition for seven days.

Faxonella were collected October 2 and placed in a stock aquarium in complete darkness at 4 PM. On the evening of October 3, 15 crayfish were placed into each of 10 pans and left in the darkroom. The average D.P.I. of 10 animals from one pan was determined at 9 AM on October 4 and at 1-hr intervals thereafter for

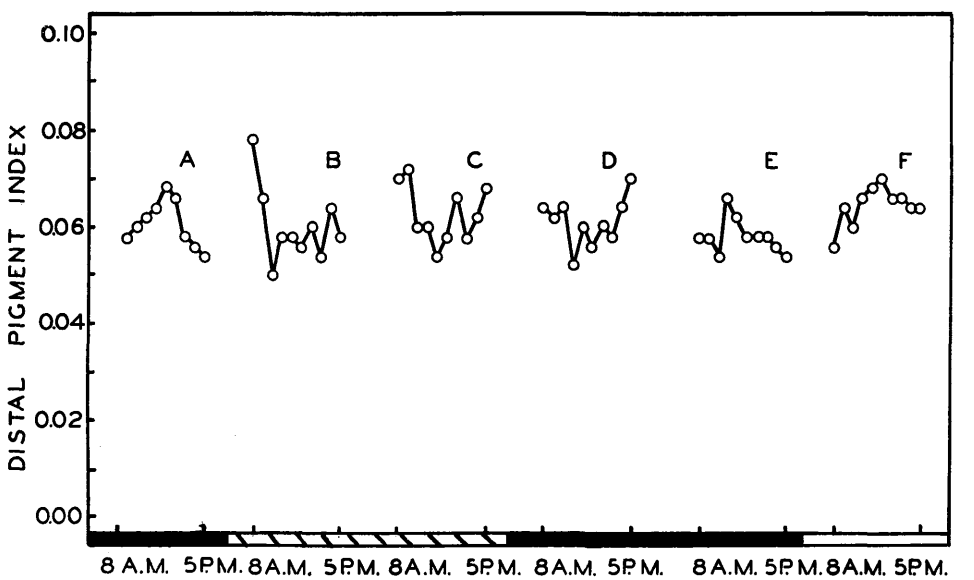

FIGURE 5. The diurnal rhythm of migration of the distal retinal pigment of crayfish subjected to reversed illumination. Black bar, crayfish were kept in constant darkness. Oblique hatchings, crayfish were placed under an illumination of 40 ft-c at 5 PM and kept there until 8 AM the next morning when the crayfish were placed in the darkroom until 5 PM. This process was repeated for 17 days. White bar, crayfish were placed in natural day-night illumination. The distal retinal pigment was determined on (A) October 4, (B) October 18, (C) October 21, (D) October 25, (E) November 1, and (F) November 8.

8 hr the average D.P.I. of the crayfish in a different pan was determined. The animals were returned to the stock aquarium after their D.P.I. was determined. The stock aquarium was then placed under an illumination of 40 ft-c at 5 PM and kept there until 8 AM the next morning when the stock aquarium was again placed in the darkroom until 5 PM. This process was done each day for 14 days. On the evening of October 17, 10 pans each containing 15 crayfish selected at random from the stock aquarium were placed in the darkroom. From 8 AM to 5 PM on October 18, the average D.P.I. of the animals was determined at 1-hr intervals.

On October 21, the average D.P.I. was again determined in the manner described above. At 8 AM on October 21 the stock aquarium was placed into the darkroom permanently. On October 25 at 7:30 AM 150 crayfish were removed from the stock aquarium and were distributed equally among 10 pans that were kept in the darkroom. The average D.P.I. of the latter animals was determined from 8 AM to 5 PM at 1-hr intervals. The average D.P.I. was again determined for the animals in darkness on November 1. On the same evening the stock aquarium was placed in a room where it would receive natural day-night illumination without artificial light at night. On the evening of November 7, 15 of these crayfish were placed into each of 10 white pans and placed into the darkroom. At 8 AM the next morning the average D.P.I. of 10 animals from one pan was determined and at 1-hr intervals thereafter for 8 hr the average D.P.I. of the crayfish in another pan was determined.

The results of the experiments are presented in figure 5 where each point represents the average D.P.I. of 10 crayfish. In table 1 the calculations were based on the maxima and minima for each set of conditions. Examination of figure 5 suggests that the reverse in illumination had probably shifted the minimum light adapted state by 12 hr. The minimum (fig. 2) of the diurnal rhythm was at 1 to 2 AM and now the minimum was at 11 AM-noon (fig. 5). When the crayfish were placed in darkness for 10 days, the abnormal rhythm exhibited a change toward a normal diurnal rhythm. Return of the normal diurnal rhythm curve occurred in crayfish kept in day-night illumination for seven days.

DISCUSSION

The migration of the distal retinal pigment demonstrated a diurnal rhythm under constant light and constant darkness in the crayfish *Faxonella clypeata*. Maximal light adaptation typically occurred at 1 PM and minimal at 1 AM. In the crayfish, *Cambarellus shufeldti*, Fingerman and Lowe (1957) reported a 24-hr rhythm of distal pigment migration based on (1) rate of dark adaptation throughout the 24-hr day, (2) response to a light exposure throughout the day, and (3) direct observation of the distal retinal pigment of crayfish exposed to constant illumination. The distal retinal pigment was most light-adapted at noon and least light-adapted at midnight. In table 1 the standard deviations for figure 3 were presented. If the apparent decline in amplitude was the result of individuals exhibiting periods which differ slightly from 24 hr, the standard deviations would increase and reflect this fact. As was apparent there was no increase in the standard deviations. However the diurnal rhythm of distal pigment migration in *F. clypeata* must be considered circadian rather than a 24-hr rhythm until very firm proof to the contrary has been provided.

Fingerman and Lago (1957) working with a population of *Faxonella clypeata* discovered that this population was divided into two groups according to the time of maximum oxygen consumption and locomotor activity. The peaks of locomotor activity and oxygen consumption were maximal about 6 AM for group A and 6 PM for group B. A secondary maximum occurred approximately 12 hr after the primary peak. Minima generally occurred about noon and midnight. The distal retinal pigment diurnal rhythm was not in phase with the activity and oxygen consumption rhythm. Comparison of the times of maxima and minima in the rhythms of distal retinal pigment, oxygen consumption, and spontaneous locomotor activity indicated that oxygen consumption and activity of *Faxonella* were maximal when the distal retinal pigment was at an intermediate state of light adaptation and minimal when at the maximum and minimum light-adapted states.

An analysis of the habitat data of 81 lots of *F. clypeata* was made by Penn (1952). Of the 81 lots he found that 84.6 per cent were collected in shallow water, less than 15 inches deep, 64.5 per cent in clear water, and 70.6 per cent were exposed to full

sunlight. The data show that the majority of specimens of *F. clypeata* live in a habitat that is clear and exposed to full sunlight. Thus at noon the illumination would be maximal and at midnight it would be minimal. Correlating this information with the diurnal distal pigment rhythm, the maximal light-adapted state occurred when the illumination was maximal and vice versa.

F. clypeata during dry periods burrow along the sides of and in the bottom of ditches instead of migrating to an adjacent slough. Ovigerous females were found in burrows regardless of conditions of the ditch, indicating that *F. clypeata* spend some part of their life cycle in burrows and thus are not exposed to illumination during the day. If the length of time the crayfish was in a burrow was long enough to inhibit the diurnal rhythm, then when the crayfish returned to natural day-night conditions of illumination the diurnal distal pigment rhythm would return. However it has been shown that a one-minute light flash at 250 ft-c can release the stored light-adapting hormone in the shrimp *Palaemonetes* (Brown, Hines, and Fingerman, 1952). Thus the animal occupying a burrow would have only to approach the entrance for a short time during midday to negate the effect of prolonged darkness. As was shown, a probable 12-hr shift in the diurnal distal pigment rhythm was corrected by seven days in normal day-night illumination (fig. 5). Animals collected during the spring, summer, and fall show a diurnal distal pigment rhythm. It is possible to account for this distal retinal pigment rhythm on the basis of an internal controlling mechanism, an endogenous clock, apparently related to the solar day.

Brown (1959) postulated that two serially coupled rhythmic centers are involved in color change in crustacea. A shift in phase in the observable rhythm by certain types of light changes was not permanent under constant conditions but drifted back over the course of a few days when the superficial center was involved. When the more basic center was shifted by other kinds of light changes, the shift now persisted indefinitely under constant conditions. Thus utilizing the two rhythmic centers hypothesis of Brown, the conclusion was drawn that illumination of daylight in the natural habitat kept the distal retinal pigment in rhythm. In the shrimps *Leander affinis* and *Anchistioides antiguensis* Kleinholz (1937) reported a double rhythm in that the distal retinal pigments show a periodicity occurring twice within a 24-hr cycle, once during the daytime when the animals were maintained in darkness, and once at night when the shrimps were kept under constant illumination. Nagano (1950) also reported a periodicity of distal pigment migration twice within a 24-hr cycle in the fresh water shrimps *Paratya compressa* and *Leander paucidens*. The results obtained with *L. affinis*, *A. antiguensis*, *P. compressa*, and *L. paucidens* indicated that not all crustacea utilize the illumination of daylight in setting the diurnal distal retinal pigment rhythm.

The length of time that the diurnal rhythm persisted in *F. clypeata* was approximately 30 days in constant light. The endogenous clock can function for a time without natural day-night illumination. If day-night illumination was one factor controlling or setting diurnal distal retinal pigment rhythm, then we would expect that if we were to reverse the day-night period of illumination, the diurnal rhythm maximal and minimal peaks would change to some other time period. Exposing the animals to light at night and keeping them in darkness during the day caused a shift in the peak by approximately 12 hr. When the animals were subjected to seven days of natural day-night illumination, the 24-hr rhythm returned. R. Smith (1948) exposed *Hemigrapsus oregonensis* to 40 hr of continuous light and then transferred them to the darkroom at 7 AM. They soon became dark-adapted and thereafter exhibited a period of dark adaptation starting at midnight and lasting until early afternoon. *H. oregonensis* in constant darkness occasionally became out of phase with the solar day during a 10 day period of observation of the 24-hr rhythm. In the shrimp *Leander serratus* the distal retinal pigment

did not exhibit any detectable persisting diurnal rhythm in constant darkness. Knowles (1950) suggested that illumination sensitizes the distal pigment cells to the hormone by which they are activated.

The diurnal distal pigment migration persisted for approximately 30 days in constant light for the crayfish *Faxonella*, whereas in *Cambarellus shufeldti* inhibition of the distal retinal pigment rhythm occurred after a week in constant light (Fingerman and Lowe, 1957). Welsh (1941) observed daily changes in the psuedopupil in *Cambarus bartoni* for four months at 21 to 23 C in darkness and for five months at 6.8 C in darkness.

SUMMARY AND CONCLUSIONS

1. The distal retinal pigment of the crayfish *Faxonella clypeata* undergoes a diurnal migration under constant conditions of light and darkness.

2. Distal retinal pigment of *Faxonella* kept under continuous illumination and darkness was maximally light-adapted at 1 PM and minimally light-adapted at 1 AM.

3. The diurnal rhythm of the distal retinal pigment continues for approximately 30 days under constant illumination.

4. The diurnal rhythm is in some way influenced by the time of day that the crayfish are exposed to light. By reversing the period of light and darkness the diurnal rhythm can be shifted out of phase with the solar-day-night rhythm.

5. The amplitude of the diurnal distal retinal pigment rhythm decreases in constant illumination and constant darkness.

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